On Growth and Form at 100

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Note

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On Growth and Form at 100

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In 2017, celebrations were held around the world to mark the centenary of D'Arcy Thompson's extraordinary book *On Growth and Form*. One of the key works at the intersection of science and the imagination, it is a book that has inspired mathematicians, biologists, artists, and thinkers as diverse as Alan Turing, Claude Lévi-Strauss, Norbert Wiener, René Thom, Henry Moore, and Ludwig Mies van der Rohe. It pioneered the science of biomathematics and has had a profound influence in art, architecture, anthropology, geography, cybernetics, and many other fields.

To mark the occasion, a three-day interdisciplinary conference was held at the neighboring universities of Dundee and St Andrews in Scotland, where D'Arcy spent almost his entire academic career and where his surviving collections are held. Delegates from around the world attended and were able to see the D'Arcy Thompson Zoology Museum in Dundee and highlights from his extensive archive of correspondence in St Andrews, as well as to hear a fascinating range of papers from mathematicians, biologists, artists, musicologists, and many others.

Born in Edinburgh in 1860, D'Arcy developed a love of nature as a boy. He entered the University of Edinburgh in 1878, intending to take a medical degree, but as his interest in biology developed, he decided to give up medicine and pursue a degree in natural science at Cambridge, where he graduated in 1883. Just a year later, he sought and won the chair of biology at the newly established University College, Dundee (now the University of Dundee).

D'Arcy quickly acquired a reputation as a wide-ranging and increasingly eccentric teacher. His successor in Dundee, Alexander Peacock, recalled:

> Fortunate were all who saw him use sketches, bits of paper and string, and soap bubbles to explain the mathematics of the honeycomb, the nautilus shell and such like … things [1].

D'Arcy admired the Germanic universities for pursuing "the idea of Universality of Knowledge," and he particularly admired the interdisciplinary work being carried out by Hans Przibram and his experimental biology team at the Vienna Vivarium, where animals were studied collaboratively by biologists, physiologists, physicists, and chemists (see [2]). In an address given to his students in 1903, D'Arcy told them:

> if you dream, as some of you, I doubt not, have a right to dream, of future discoveries and inventions, let me tell you that the fertile field of discovery lies for the most part on those borderlands where one science meets another … Try also to understand that though the sciences are defined from one another in books, there runs through them all what philosophers used to call the *commune vinculum*, a golden interweaving link, to their mutual support and interpretation [3].

It would be precisely this interweaving link that D'Arcy would demonstrate so powerfully in his masterpiece *On Growth and Form*. The seed was planted in 1889, when he wrote to one of his students: "I have taken to Mathematics, and believe I have discovered some unsuspected wonders in regard to the Spirals of the Foraminifera!" [4]. D'Arcy became increasingly convinced that the laws of mathematics could be used to explain the growth and form of living organisms. This was a highly controversial idea. Many had come to accept Darwin's theories of evolution by natural selection as the solution to all of the remaining questions about life, but D'Arcy was less certain. He admired Darwin greatly and managed to persuade him to write the preface to his first publication, a translation of Hermann Müller's *The Fertilisation of Flowers*, published in 1883, shortly after Darwin's death. But at the British Association meeting in 1894, D'Arcy gave a paper entitled "Some Difficulties in Darwinism," in which he proposed that "laws of growth" could explain the many forms and colors of animals like hummingbirds, rather than any perceived "struggle for existence" [5]. In *On Growth and Form* he went further, quoting Francis Bacon to state:

> So long and so far as "fortuitous variation" and the "survival of the fittest" remain engrained as fundamental and satisfactory hypotheses in the philosophy of biology, so long will these "satisfactory and specious causes" tend to stay "severe and diligent inquiry," "to the great arrest and prejudice of future discovery" [6].

Having been initially reluctant to share such views, it was not until 1908 that D'Arcy published anything detailed on the topic: a paper in *Nature* on "The Shape of Eggs and the Causes Which Determine Them" [7]. Two years later, the botanist Albert Seward asked him to write a small book on whales for the Cambridge Manuals of Science and Literature, a series of popular works priced at a shilling each. D'Arcy wrote back to Seward:

> I do not much care about the subject of "Whales" … On the other hand, I have had an idea in my head for

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> a long time of a little book with some such title as "The Form of Organisms," or "Growth and Form" … If this subject commends itself to you, I will set to work upon it, but I can only do so at odd moments, and I cannot safely promise you the little book sooner than say six or eight months hence [8].

The more he considered the subject, however, the larger and more daunting it became. In 1911, he told zoologist F.W. Gamble:

> I engaged to write my little book, mainly because its size was so small, and because I thought one could condense into it what was pretty certainly known, while if one wrote a larger book one would be led into the endless discussion of debatable matter. But I am already beginning to find that it is equally difficult to discover where the subject ends, and where certainty begins [9].

Later that year, he raised some aspects of the subject in an address to the annual meeting of the British Association, and it was there that he first made his much-quoted analogy that "the form of an object is a 'diagram of Forces,'—in this sense, at least, that from it we can judge or deduce the forces that are acting or have acted upon it" [10].

But little else emerged until 1914, when he gave a paper to the Royal Society of Edinburgh on "Morphology and Mathematics," which introduced for the first time his iconic transformation diagrams [11]. D'Arcy's biggest problem was lack of time: as well as his teaching and administrative duties in Dundee, he was taking on a huge workload as scientific expert for the Fishery Board of Scotland and as a prime mover in the International Council for the Exploration of the Sea. *On Growth and Form* may never have appeared at all had the Great War not reduced D'Arcy's workload significantly, bringing much of his international fisheries work to a standstill and significantly cutting the number of students he had to teach. Writing to his friend Marcus Hartog (a zoologist in Cork), he noted that the war "has brought me comparative leisure to undertake a very laborious job." Despite the difficulty, D'Arcy claimed:

> I do not repent of undertaking the job, because most of our brother biologists still need to be told that there is such a thing as physical science and that you cannot spin either rope or cobweb without it [12].

In May 1915, D'Arcy announced: "I have practically finished my book … It represents some 20 years of work and thought, and I have great hopes that it will be found useful [13]." D'Arcy had drawn extensively on the resources available to him in Dundee, including the specimens in his zoology museum and the expertise of his present and past colleagues, particularly the physics professor William Peddie and the engineering professor Thomas Claxton Fidler, both of whom reviewed his text in detail and contributed numerous ideas and illustrations. His assistant Doris Mackinnon and one of his former students, Helen Ogilvie, contributed many more of the book's diagrams.

Partly due to wartime paper shortages and partly due to D'Arcy's insistence on numerous last-minute changes, *On Growth and Form* was finally printed only in March 1917. At the end of the book, D'Arcy lays down the gauntlet for future research:

> while I have sought to shew the naturalist how a few mathematical concepts and dynamical principles may help and guide him, I have tried to shew the mathematician a field for his labour, – a field which few have entered and no man has explored.

If he was hoping for a rush of eager biomathematicians to start exploring the field, he was to be disappointed. Only a handful of significant works followed over the next two decades, many of them in the area of ecology and population dynamics, which began to make extensive use of mathematical modeling.

Writing in 1931, D'Arcy argued:

> There are innumerable biological problems with a mathematical bearing; but the mathematics required is mostly of too high an order for the biologist. Nothing is more wanted in biology than that mathematicians of first-class standing should interest themselves in biological problems [14].

D'Arcy himself felt that he could not take his mathematical research further; he told one of his Cambridge friends, the mathematician and physicist Joseph Larmor, "I am … handicapped, as always, by my now irremediable ignorance, especially of (elementary) mathematics [15]." However, he worked hard to promote and support the work of others, including the Italian Vito Volterra, the Russian Vladimir Kostitzin, the Briton Dorothy Wrinch, and the Ukrainian Nicolas Rashevsky.

The most significant developments in biomathematics would, of course, come long after D'Arcy's death in 1948. The development of computers coupled with the rise in popularity of evolutionary developmental biology (evo-devo) brought D'Arcy's work back into the mainstream. The University of Dundee is just one of many institutions around the world teaching and researching mathematical biology, looking at the mathematical modeling of cancer cells and starling murmurations among others. The mathematics used may be completely different from anything contemplated by D'Arcy, but the lineage is clear.

For our centenary conference we were delighted to have two exceptional keynote speakers, whose presentations we publish here. Stephen Wolfram is an internationally renowned computer scientist and physicist. Best known as the creator of Mathematica and the Wolfram language, he is the author of *A New Kind of Science* [16] and the founder and CEO of Wolfram Research. Over the course of nearly four decades, he has been a pioneer in the development and application of computational thinking. His early work on complexity in nature led him to study the behavior of simple computer programs known as cellular automata. In his paper, he shows how these can help realize D'Arcy Thompson's ideas for the development of form.

Evelyn Fox Keller is one of the most internationally respected historians of science. A physicist, author, and feminist, she is currently professor emerita of the history and philosophy of science at MIT. Beginning her career in theoretical physics, she moved on to work in molecular biology before becoming renowned for her work as a feminist critic of science. Over the years she has documented how the masculine-identified public sphere and the feminine-identified private sphere have structured thinking in two areas of evolutionary biology: population genetics and mathematical ecology. Her concern is to show how the selection process that occurs in the context of discovery limits what we come to know. Her books include *Keywords in Evolutionary Biology* [17], *The Century of the Gene* [18], and *Making Sense of Life: Explaining Biological Development with Models, Metaphors, and Machines* [19]. The latter has a particular focus on mathematical biology, and in her paper she brings that work up to date, discussing the legacy of D'Arcy Thompson's work today. While for much of the twentieth century *On Growth and Form* was dismissed because of its apparent dismissal of genetics, now it can offer invaluable insight toward a more holistic view in which physics and mathematics are vital tools in understanding biology.

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